

More than the sum of the parts: annual partitioning within spatial guilds underpins  
community regulation

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## Abstract

To withstand the pressures of a rapidly changing world, resilient ecosystems should exhibit compensatory dynamics, including uncorrelated temporal shifts in population sizes. The observation that diversity is maintained through time in many systems is evidence that communities are indeed regulated and stabilized, yet empirical observations suggest that positive covariance in species abundances is widespread. This paradox could be resolved if communities are composed of a number of ecologically relevant sub-units in which the members compete for resources, but whose abundances fluctuate independently. Such modular organization could explain community regulation, even when the community as a whole appears synchronized. To test this hypothesis, we quantified temporal synchronicity in annual population abundances within spatial guilds in an estuarine fish assemblage that has been monitored for 36 years. We detected independent fluctuations in annual abundances within guilds. In contrast, the assemblage as a whole exhibited temporal synchronicity - an outcome linked to the dynamics of guild dominants, which were synchronized with each other. These findings underline the importance of modularity in explaining community regulation and highlight the need to protect assemblage composition and structure as well as species richness.

## Introduction

One of the major challenges in ecology is explaining how diverse communities maintain their properties through time. We know that (substantially transformed habitats apart) assemblage diversity does not systematically change over the time scale of years to decades [1-4]. Indeed, there is now evidence that assemblage size (richness and total abundance) is regulated [5]. In principle, compensatory dynamics [6, 7], whereby increases in the abundances of one taxon are offset by decreases in another, should promote persistence. Nonetheless, where tests have been carried out, species tend towards positive temporal covariance in abundance with synchronized rises and falls in numbers [8].

May's pioneering work showed that randomly assembled ecosystems are unstable [9, 10]. However, species interactions in ecological communities have been shaped by evolution, and new theory [11] suggests that higher-order interactions (where one species mediates the interactions of other species) can support species coexistence.

Modularity, defined here as coherent sub-groups of entities such as those with a shared function or habitat, can also potentially underlie resilience in domains ranging from engineering to banking systems [9, 12]. Indeed, there is evidence that systems with inherent modularity, such as mutualistic networks of plants and their pollinators, and foodwebs [13], can be stable. A recent experimental study [14] showed that modularity promotes the persistence of an arthropod population. Much of the focus on modularity in natural communities has been directed towards the role tightly organized networks of species, such as mutualisms, play in promoting stability. Yet ecosystems contain many other looser associations of taxa with the potential to provide a form of modularity that supports community regulation. Indeed, Gotelli et al. [5] argue that the regulation of entire communities could be linked to these looser groupings. One form of modularity arises when species subdivide into spatial guilds associated with different habitat zones. In the Bristol Channel estuarine fish assemblage, for example, species form guilds that exploit the habitat in different ways. These guilds include fish in the pelagic zone and those associated with hard

50 benthic surfaces [15]. Guild structure has been stable for the almost 4 decades over which the system has been monitored [16].

To test the hypothesis that modularity promotes coexistence, we draw on this exceptionally complete estuarine assemblage dataset, in which the abundances of the  
55 fish species present have been monitored, every month, using the same methodology, for 36 years. We focus on the species that occur persistently (that is, are present in at least 10 years) as these account for most of the abundance in the system [17], and have dynamics that are shaped by density dependence [18]. We quantify the degree of synchronicity of annual populations in the overall assemblage (the four main spatial  
60 guilds combined), and then within guilds. In this context synchronicity is a measure of the extent to which the abundances of species covary over time. Annual abundance measures the success of a species in a given year, taking into account seasonal dynamics (which vary amongst species in this system [19]). It is also the temporal unit used in many studies of biodiversity change and assemblage regulation [5]. The  
65 dominant species in each guild are spatially segregated from one another, yet, because they appear be responsive to shared external drivers [20], could be key players in producing synchronous dynamics in the assemblage as a whole. We therefore additionally evaluate synchrony in annual abundance amongst the dominants.

## 70 Methods

The Bristol Channel estuarine fish community has been sampled monthly for 36 years; 84 species and >200,000 individuals have been recorded. Fish samples are collected from the cooling water filter screens at Hinkley Point B Power Station,  
75 situated on the southern bank of the Bristol Channel in Somerset, England. The water intakes are in front of a rocky promontory within Bridgwater Bay. Depending upon the tide, the fish were sampled from water varying in depth from about 8 to 18 m. For a full description of the intake configuration and sampling methodology see [21, 22]. Methodology has not changed over the 36 years of study since monthly quantitative  
80 sampling commenced in January 1981. The total volume of water sampled per month, which has not varied over the entire period, is  $4.27 \times 10^5 \text{ m}^3$ . To standardize for tidal influence, all sampling dates are chosen for tides halfway between springs and neaps, with sampling commencing at high water (normally about 12.00 hrs). Fish are collected hourly for a 6 h period, identified to species, measured, weighed and the  
85 number of individuals recorded.

Our analysis focuses on the  $S=33$  persistent species (i.e. those present in at least 10y) in the four main spatial guilds (hard benthic, soft benthic, pelagic and proximo benthic, see also SI Table1) as defined in [15, 16, 18]. Guild dominants (Conger  
90 *Conger conger*, flounder *Platichthys flesus*, sprat *Sprattus sprattus*, and whiting, *Merlangius merlangus*) are the species that account for most of the biomass within their guild, as well as within the entire assemblage (average 70.3% of total sampled annual fish biomass for the 4 guild dominants for the years 2000 – 2011, maximum 80.4 %, minimum 42.5%). These are species for which the Bristol Channel lies  
95 towards the centre of their geographical range, and that are well-adapted to local conditions.

Synchrony is quantified using Loreau's method [23]. Loreau's method (introduced by Loreau and de Mazancourt in 2008 [23]) is based on the relationship between the

100 variance in the abundance of the entire community, and the variances of the  
abundances of the species that make up the community [23, 24]. It is 0 when perfect  
asynchrony prevails. As the average temporal correlation between species increases,  
so does the value of the metric, with 1 denoting perfect synchrony. In addition, we  
105 calculate Tilman's index of community stability [25]. This index evaluates community  
stability by dividing mean abundance over the time frame of interest, by the temporal  
standard deviation.

Calculations are made using the R package Codyn [24, 26]. In all cases observed data  
are tested relative to a null model of independence in temporal abundance, based on a  
110 cyclic shift randomization [27] that preserves temporal autocorrelation within species,  
but breaks temporal cross-correlations amongst species. A cyclic-shift permutation  
takes a random start date for the sequence of annual abundances for a given species,  
and 'wraps' the abundances around to the start of series as required. A cyclic-shift  
permutation is more ecologically realistic than a free permutation. Preserving species  
115 temporal autocorrelation is important here, given the role that density-dependent  
dynamics play in this system [18].

In essence our analysis is as follows. We select a guild (as previously defined [15,  
16]) and compute each metric using the observed data. We then permute all of the  
120 species in that guild  $j$  times and calculate metrics for each permutation. Next, we  
examine the quantile value of the observed metric relative to the null distribution of  
cyclic shifted metrics (Figure S2). This analysis is repeated for the assemblage as a  
whole, and for dominant taxa separately. Data are not transformed for these analyses.

125 To determine if synchrony is higher or lower within guilds than would be expected  
from a random assemblage of species, we draw  $S$  species at random,  $i$  times, from the  
overall assemblage, and compute the metric for each  $i$ th group. This analysis  
illustrates how the value of the metric varies with  $S$  in a system with this structure  
(Figure 3). We then expose each of these  $i$  groups to  $j$  cyclic shift permutations, as  
130 before. The next step is to compute the  $Z$  score of the  $i$ th metric in relation to the  
distribution of  $j$  cyclic shifted metrics. Finally, we plot the distribution of the  $i$   $Z$   
scores, for the  $S$  species, and ask how the  $Z$  score of observed guild, based on the null  
expectation of the cyclic shift (as above), compares. In other words, is the extent of  
synchrony in a guild of given  $S$  different from a synthetic guild of equivalent size,  
135 when both have been tested using the cyclic shift protocol? We do not run these  
additional randomisations on the overall assemblage as there is only one possible  
draw of  $S=33$  species. To ascertain whether seasonal patterns take the same form as  
annual ones we also compute the cyclic shift permutation using monthly data.

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## Results

145 The species in each guild can be ranked from more common to less common - a  
typical pattern in ecological assemblages (Figure 1). Annual abundances fluctuate  
with a rise in one year often being matched by a fall in the subsequent year (Figure 1).

The impression, from visual inspection of these plots (Figure 1e), that there is  
stronger positive covariance in annual abundance amongst the dominant species than

150 within the four guilds (Figure 1a-d), is supported by the analysis. As Figure 2 shows,  
synchronicity in the annual abundances of the dominant taxa is greater than would be  
expected by chance. The combined assemblage also exhibits statistically significant  
synchronicity even though the species within each of the guilds have dynamics that  
155 are consistent with independent fluctuations. The same result emerges from the  
analysis of community stability. Thus, when viewed as a whole, the assemblage  
appears less stable [25], and more highly synchronized than it does if it is considered  
as a composite of functionally distinct modules.

The value of both metrics varies with  $S$  (Figure 3). However, our additional  
160 randomisation tests confirm that the results we report are not an artefact of reduced  $S$   
within guilds compared to the whole assemblage (Figure S3). Here we find that the  
dominant taxa exhibit greater synchrony in annual abundance, but intriguingly also  
higher stability, than the null expectation based on randomly drawn guilds of equal  $S$ ,  
subjected to a cyclic permutation (Figure S3). In contrast, the degree of synchrony  
165 and stability in each of the guilds is consistent with the expectation of independent  
fluctuations in the annual abundances of guild members.

Although the focus of our study is on annual abundance we find broadly the same  
result if we analyse the same groupings of species using monthly data ( $n=442$  time  
170 points). When month by month abundances are considered, the dominant species, the  
overall assemblage, as well as the proximo benthic guild, show greater temporal  
synchrony and less stability than expected by chance (Figure S4). In contrast, the hard  
benthic, soft benthic and pelagic guilds continue to display independent fluctuations  
in abundance, and retain stability, at this finer temporal resolution (Figure S4),  
175 indicating that these patterns are not restricted to single time scales.

## 180 Discussion

Our results uncover a plausible mechanism to account for the persistence and  
regulation of ecological communities. By partitioning the assemblage into functional  
groupings we can explain how community properties are maintained despite overall  
temporal covariance in species abundances. The pattern we see is not one of  
185 compensatory dynamics *sensu stricto* because that would imply stability to be greater  
within guilds than for either the randomly permuted guilds or randomly assembled  
guilds - something we did not detect in these data. Instead, we find independent  
fluctuations in species abundances within guilds - groups of fish that interact with one  
another and share the same habitat. Loreau's synchrony metric is most heavily  
190 influenced by abundant species [23, 24]. Since dominant species jointly account for  
the largest fraction of the assemblage's abundance it is their synchronicity that appears  
to be driving the synchronicity of the assemblage as a whole. However, as our study  
shows, because community diversity is the product of the dynamics of the constituent  
units (here spatial guilds) it reflects more than the sum of the parts.

195 The analysis also uncovers an intriguing, and in some ways counter-intuitive finding,  
due to the contrasting insights provided by the different null model approaches. When  
we shuffle the individual guilds, and the group of dominants, using the cyclic shift  
permutation, we are preserving the temporal dynamics of each species in the system

(within-species temporal autocorrelation) but breaking correlations between species abundances. In this context, synchrony and stability results are mirror images of one another in all cases (i.e. increased synchrony results in reduced stability, relative to the null expectation (Figure 2)). However, when we construct synthetic groupings by drawing  $S$  species at random from the assemblage as a whole, the dominant species appear to be both synchronous and stable (albeit not falling outside the 95% limits of the null distribution - Figure 3), while the individual guilds exhibit the same pattern as before. Note that the observed values for the 2 metrics are the same in Figures 2 and 3, but the shape of the null distribution differs.

We suggest that because the dominant species are spatially segregated in the system, they can each respond to the same environmental drivers without directly competing with one another, thus there is no advantage in avoiding synchronicity. Because the dominants are limited by carrying capacity constraints they respond synchronously to changes in environmental parameters that alter overall ecosystem production and resource availability. As such, their dynamics appear relatively synchronous and relatively stable when viewed against the backdrop of a randomly assembled guild. However, if we remove the natural cross-correlations in temporal abundance in this group of dominants (via the cyclic shift permutation - Figure 2) we find that synchronicity is high and stability is low. The influence of the cross correlations in abundance seems strong given the result obtained in the hybrid null model (Figure S3). As we have noted previously, the most dominant species show the least temporal variation in abundance [18], suggesting that they will be relatively more stable than a randomly assembled group of species, as long as their natural dynamics and cross-correlations in abundance, are preserved. This analysis highlights the utility of the null model approach [28, 29] in elucidating the mechanisms that structure ecological communities.

Competition between species within spatial guilds [19], makes temporal partitioning in the abundance of guild members likely. Pairwise correlations in annual abundance occur within all guilds, as well as amongst the dominant species (Figure S5), and some interesting, but different, patterns emerge. Although the dynamics of the dominant species are mediated by similar environmental drivers [20], spatial partitioning associated with guild membership means that direct competition amongst them for spatial and trophic resources will be muted [19].

Independent fluctuations in temporal abundance within a guild will reduce variability of aggregate guild properties, through statistical averaging [30], also known as the portfolio effect [31]. But the portfolio effect alone cannot account for within guild dynamics, because guild members are more seasonally dispersed than would be expected by chance [19]. The marked unevenness in species abundances in guilds (Figure 1) will also moderate the influence of the portfolio effect [30, 31]. Indeed, intra-guild variability in species responses to environmental conditions, combined with interspecific competition [18, 19] suggests that species interactions play an important role in temporal structuring. As such, the annual dynamics of these guilds are consistent with the insurance effect [30]. The uncorrelated temporal dynamics within guilds could also reflect a straightforward diversity or sampling effect.

The importance of compensatory dynamics in promoting community stability is widely recognized, but only sparsely supported by data [7, 8]. One reason for this

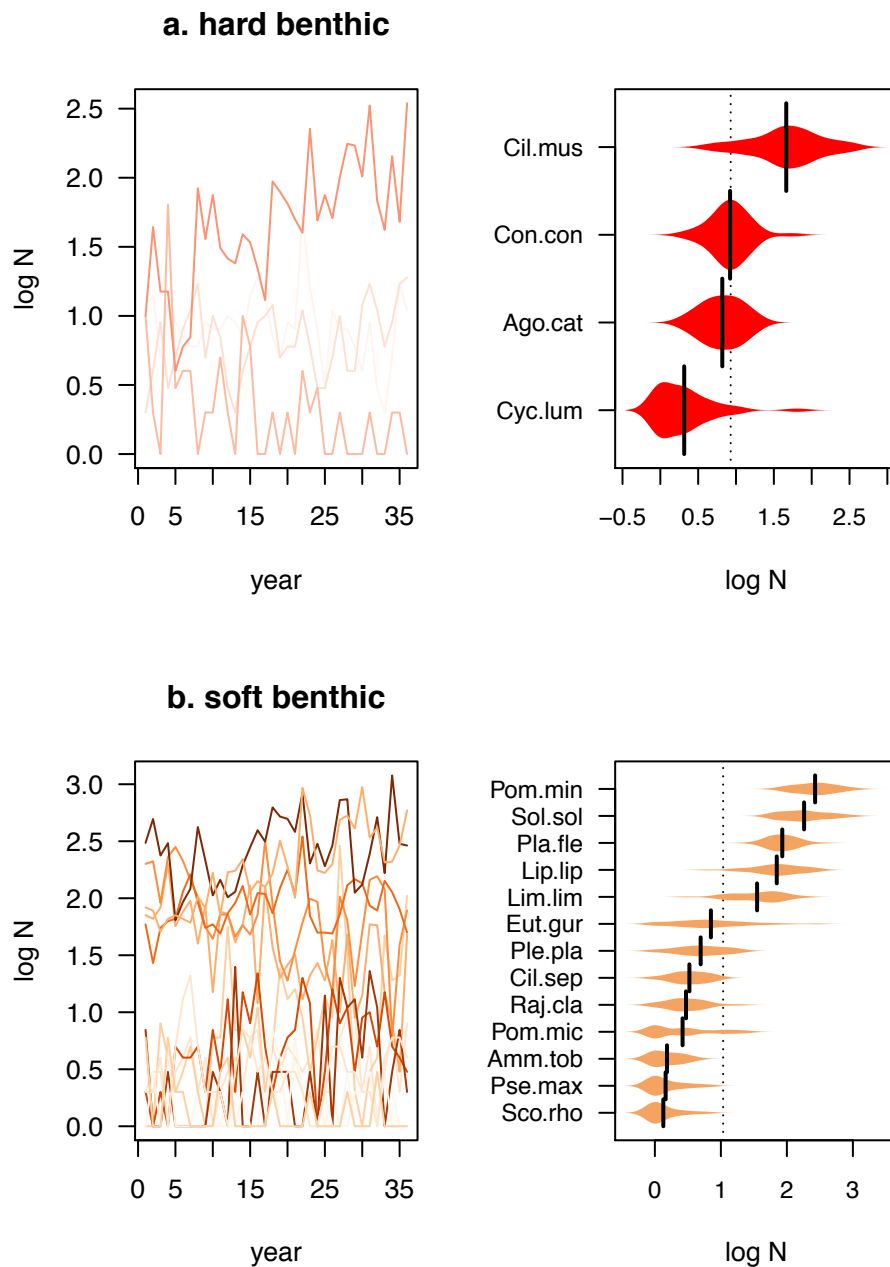
could be that aggregate communities are typically probed in meta-analyses of large databases. However, evidence for compensation appears strongest when assemblages are decomposed, for example by taking account of variation in ecophysiology [32] or habitat heterogeneity [33]. Detailed local knowledge of taxa thus remains an essential part of community ecology alongside broad brush macroecological analyses.

Our approach is transferable to other ecosystems where communities of species are divisible into functional ecological groups. For example, taxa that form the gut microbiome may occupy spatial guilds within the intestine [34] suggesting that the decomposition we discuss here could shed light on the complex dynamics of this diverse microbial system. The guild approach offers a tractable means of extending the search for the mechanisms that underpin species coexistence beyond pairwise interactions [35]. Finally, our results underline the importance of protecting entire assemblages, as community resilience is supported by locally-adapted complexes of species. In practice, conservation effort is often focused on safeguarding populations of iconic species rather than on protecting the ecological assemblages in which they occur. Care needs to be taken to ensure that such species-specific conservation, and the attendant habitat management, does not weaken or reduce the natural modularity essential for resilient, healthy, ecosystems.

#### Ethics statement

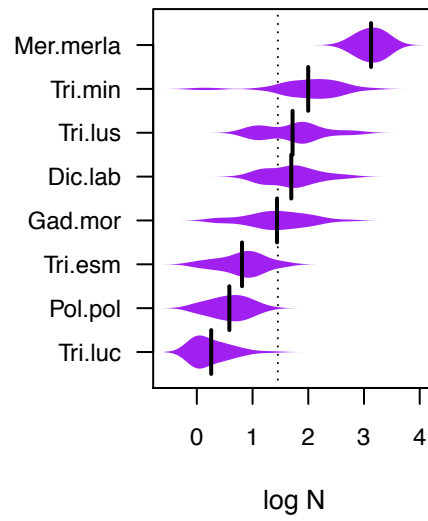
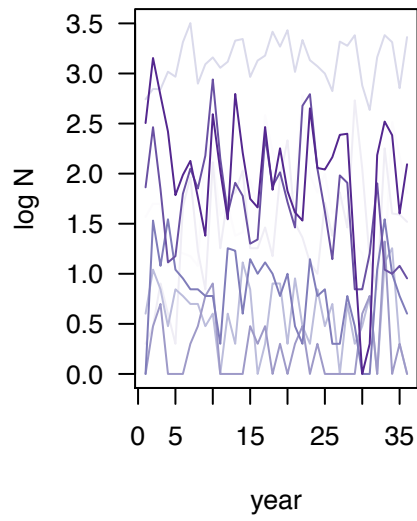
The work complied with Association for the Study of Animal Behaviour / Animal Behavior Society Guidelines for the Use of Animals in Research and legal requirements of the UK where the work was carried out, and all institutional guidelines.

Figure 1. Annual abundances of the species in the four guilds (a. hard benthic, b. soft benthic, c. proximo benthic, d. pelagic) and the dominant taxa (e.). Abundance data are transformed ( $\log_{10}(X+1)$ ) prior to plotting. In each case the left panel shows the time series of the annual abundances of the species in the group, while the right panel ranks the species from most to least abundant and uses a bean plot [36] to illustrate temporal variation in the abundance of that taxon. Mean values are shown for the overall line and bean lines. Species abbreviations can be found in Table S1. See Figure S1 for a combined time series plot for all species in the analysis and [36] for details of the methodology used to compute density in the beanplots.

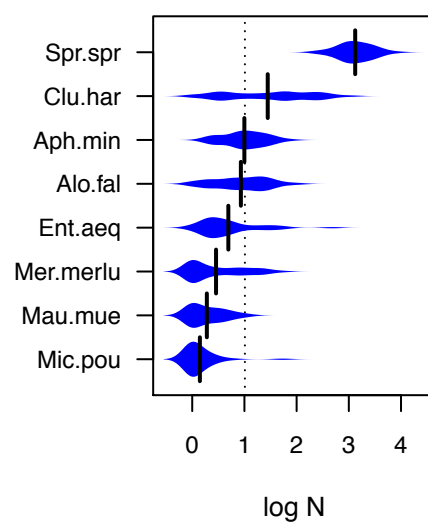
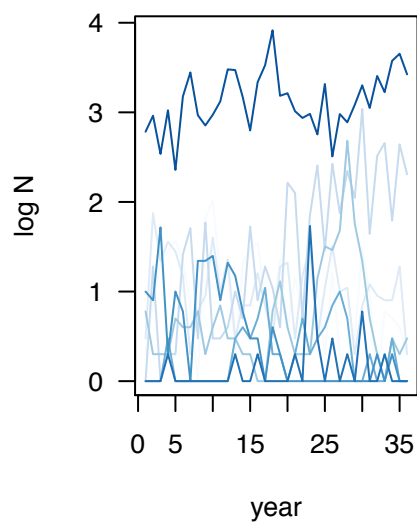




### c. proximo benthic



### d. pelagic



### e. dominants

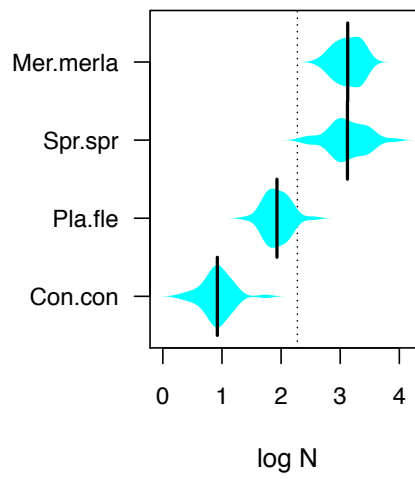
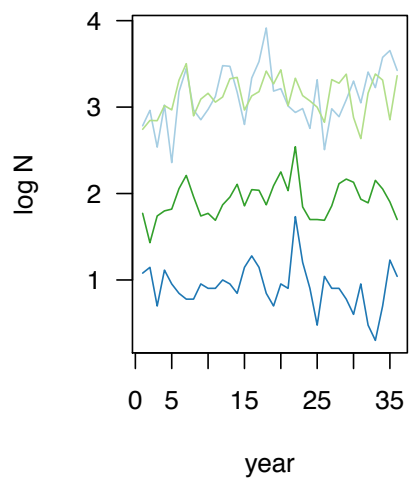


Figure 2. Bean plots illustrating the null distribution of synchrony values (Loreau index [23]) and community stability (Tilman index [25]), based on a cyclic shift randomisation (1000 draws, using the *shuffle\_community* function in Codyn [24]) of species temporal abundances in: hb (hard benthic guild); sb (soft benthic guild); pb (proximo benthic guild); pel (pelagic guild), all (combined guilds, S=33); dom (dominant species in 4 spatial guilds). Only species present  $\geq 10$ y are included. In each case a black dot represents the observed value. The quantiles of these are as follows: synchrony - hb=0.522; sb=0.893; pb=0.811; pel=0.475; dom=0.994; all=0.993, stability - hb=0.478; sb=0.107; pb=0.189; pel=0.525; dom=0.006; all= 0.007. The dotted lines show the overall mean value. (See Figure 1 for information on bean plots.)

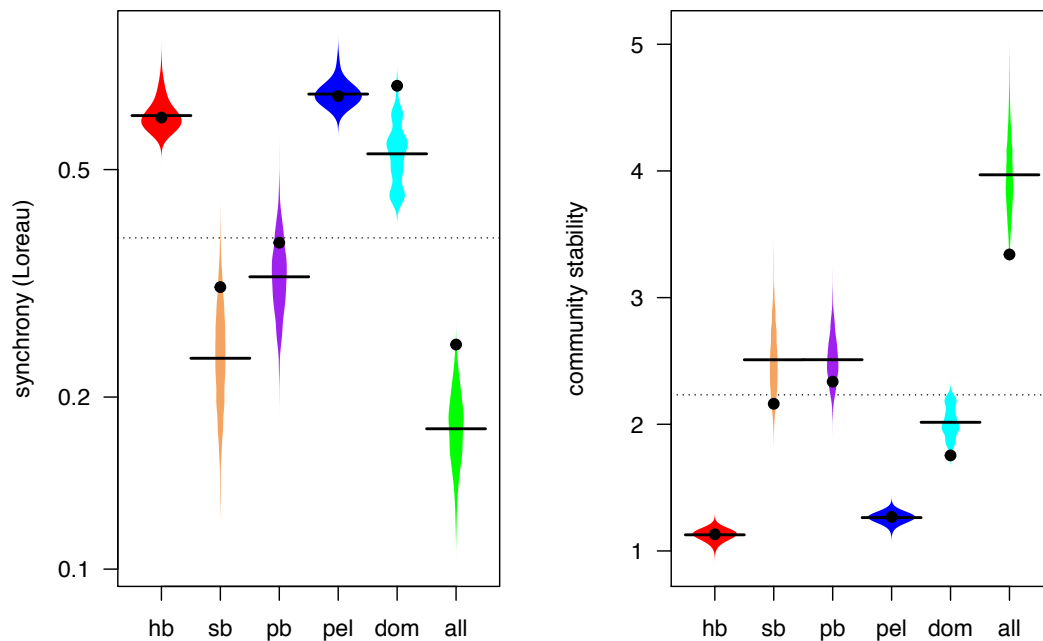
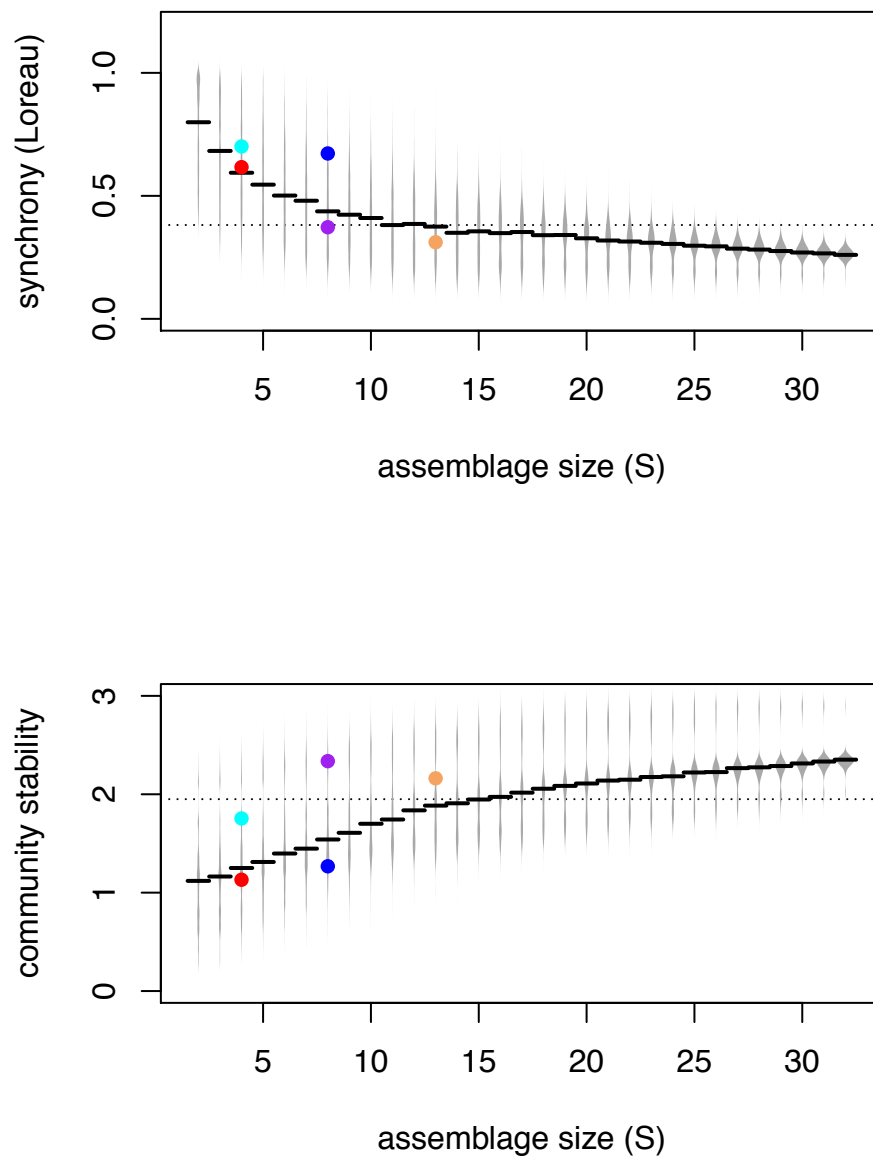


Figure 3. Relationship between metric (top: synchrony; bottom: community stability) and assemblage size. In these plots the null distribution (illustrated as bean plots) consists of 1000 random draws of species at each assemblage size ( $S=2$  to  $S=32$  species). (See Figure 1 for information on bean plots.) The observed values for each group of fish are superimposed on these bean plots. Note that the observed values are the same as those in Figure 2, as is the colour coding (hard benthic (red); soft benthic (orange); proximo benthic (purple); pelagic (dark blue); dominants (cyan)), but that a different null distribution is used in Figure 3 (see text for details).



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# More than the sum of the parts: annual partitioning within spatial guilds underpins community regulation

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## Supplementary Material

1. Table 1 Guild species list.
2. Data availability.
3. Figure S1 Time series plot for combined species.
4. Figure S2 Summary of approach used in randomisation tests.
5. Figure S3 Z scores for observed guilds from a null distribution using a cyclic shift randomisation, in relation to the distribution of Z scores obtained using synthetic guilds of equivalent *S*.
6. Figure S4 Synchrony and community stability analysis using monthly data.
7. Figure S5 Distribution of correlation coefficients (Pearson), showing temporal correlation between pairs of species in group or guild of interest.

### 1. Table S1 – The 33 guild members

Species	Common name	Abbreviation	Guild
1. <i>Agonus cataphractus</i> (L.)	Hooknose (Pogge)	Ago.cat	HARD BENTHIC
2. <i>Ciliata mustela</i> (L.)	Rockling,5-Bearded	Cil.mus	HARD BENTHIC
3. <i>Conger conger</i> L.	Conger	Con.con	HARD BENTHIC
4. <i>Cyclopterus lumpus</i> L.	Lumpsucker	Cyc.lum	HARD BENTHIC
5. <i>Alosa fallax</i> (Lacepede)	Shad,Twaite	Alo.fal	PELAGIC
6. <i>Aphia minuta</i> (Risso)	Goby,Transparent	Aph.min	PELAGIC
7. <i>Clupea harengus</i> L.	Herring	Clu.har	PELAGIC
8. <i>Entelurus aequoreus</i> (L.)	Snake pipefish	Ent.aeq	PELAGIC
9. <i>Maurolucus muelleri</i> (Gmelin)	Pearlsides	Mau.mue	PELAGIC
10. <i>Merluccius merluccius</i> (L.)	Hake	Mer.merlu	PELAGIC
11. <i>Micromesistius poutassou</i>	Blue Whiting	Mic.pou	PELAGIC
12. <i>Sprattus sprattus</i> (L.)	Sprat	Spr.spr	PELAGIC
13. <i>Dicentrarchus labrax</i> (L.)	Bass	Dic.lab	PROXIMO BENTHIC
14. <i>Gadus morhua</i> L.	Cod	Gad.mor	PROXIMO BENTHIC
15. <i>Merlangius merlangus</i> (L.)	Whiting	Mer.merla	PROXIMO BENTHIC
16. <i>Pollachius pollachius</i> (L.)	Pollack	Pol.pol	PROXIMO BENTHIC
17. <i>Trigla lucerna</i> L.	Gurnard,Tub	Tri.luc	PROXIMO

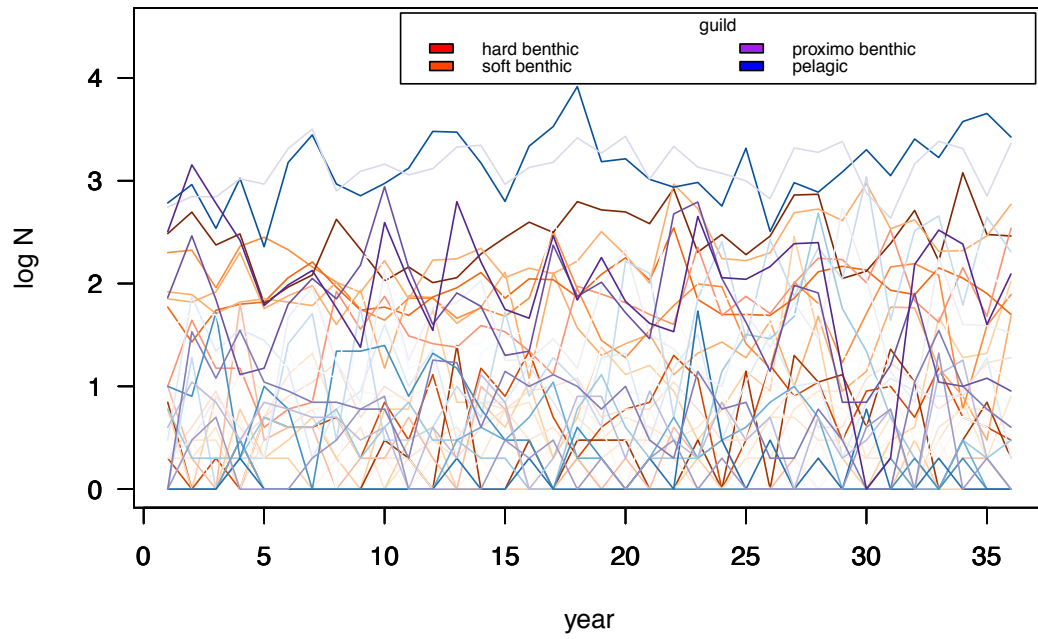
			BENTHIC
18. <i>Trisopterus esmarkii</i>	Norway pout	Tri.esm	PROXIMO BENTHIC
19. <i>Trisopterus luscus</i> (L.)	Pout	Tri.lus	PROXIMO BENTHIC
20. <i>Trisopterus minutus</i> (L.)	Poor cod	Tri.min	PROXIMO BENTHIC
21. <i>Ammodytes tobianus</i> L.	Sand eel, Common	Amm.tob	SOFT BENTHIC
22. <i>Ciliata septentrionalis</i> (Collet)	Rockling, Northern	Cil. sep	SOFT BENTHIC
23. <i>Eutrigla gurnardus</i> (L.)	Gurnard, Grey	Eut.gur	SOFT BENTHIC
24. <i>Limanda limanda</i> (L.)	Dab	Lim.lim	SOFT BENTHIC
25. <i>Liparis liparis</i> (L.)	Sea snail, Common	Lip.lip	SOFT BENTHIC
26. <i>Platichthys flesus</i> (L.)	Flounder	Pla.fle	SOFT BENTHIC
27. <i>Pleuronectes platessa</i> L.	Plaice	Ple.pla	SOFT BENTHIC
28. <i>Pomatoschistus microps</i> (Kroyer)	Goby, Common	Pom.mic	SOFT BENTHIC
29. <i>Pomatoschistus minutus</i> (Pallas)	Goby, Sand	Pom.min	SOFT BENTHIC
30. <i>Psetta maxima</i> (L.)	Turbot	Pse.max	SOFT BENTHIC
31. <i>Raja clavata</i> L.	Ray, Thornback (Roker)	Raj.cla	SOFT BENTHIC
32. <i>Scophthalmus rhombus</i> (L.)	Brill	Sco.rho	SOFT BENTHIC
33. <i>Solea solea</i> L.	Sole (Dover sole)	Sol.sol	SOFT BENTHIC

A further 11 species occurred persistently in the assemblage: *Scyliorhinus caniculus* (L.); *Gasterosteus aculeatus* L.; *Mullus surmuletus* L.; *Atherina boyeri* Risso; *Trachurus trachurus* (L.); *Syngnathus acus* (L.); *Gobius niger* L.; *Syngnathus rostellatus* Nilsson; *Callionymus lyra* L.; *Liza ramada* (Risso); *Anguilla anguilla* (L.). These species are associated with different habitats or are passage migrants.

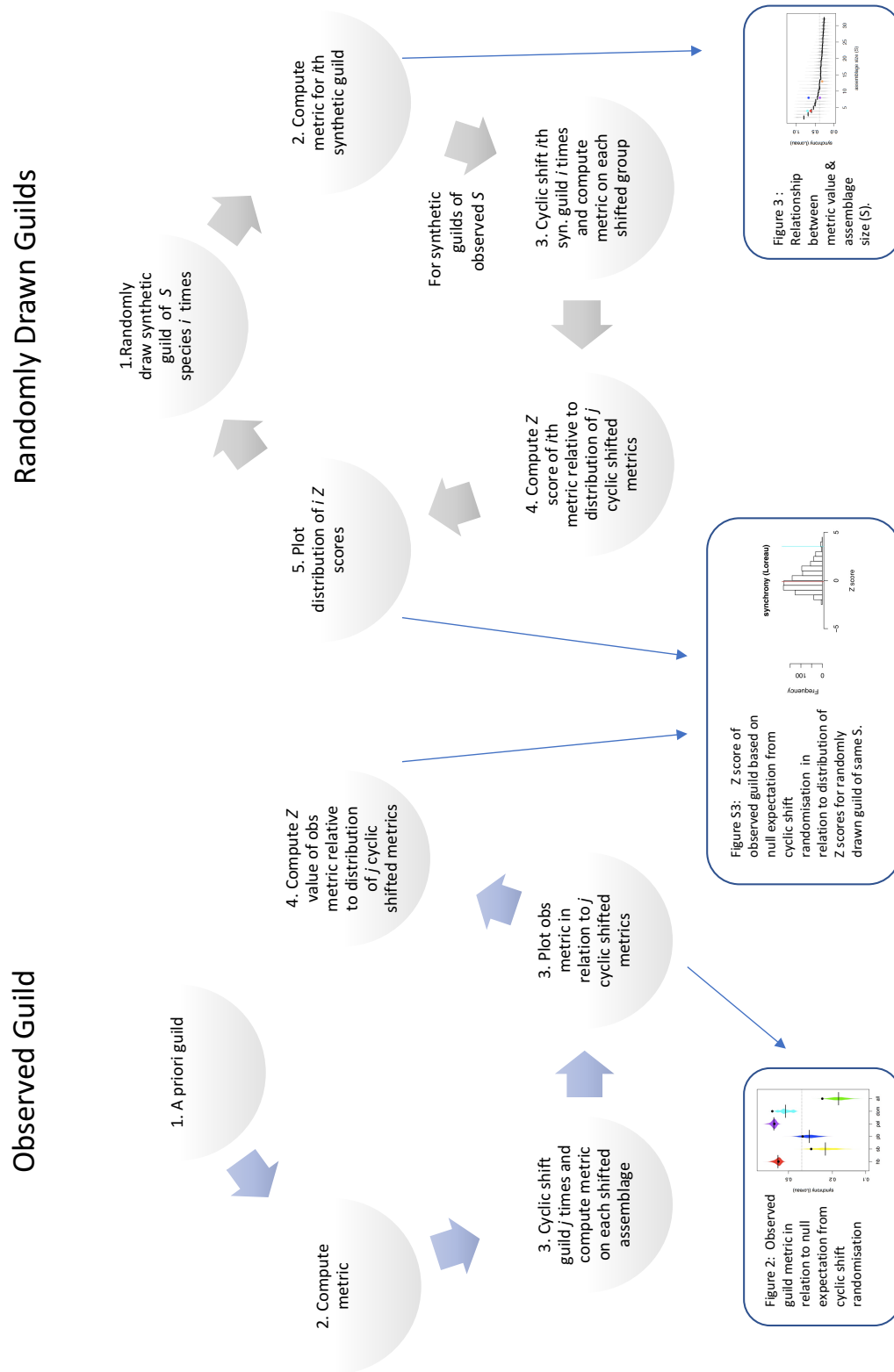
2. Data availability. Data are available at: <https://dx.doi.org/10.17630/e678f99b-e170-4852-bf70-ab738c6a81b7>



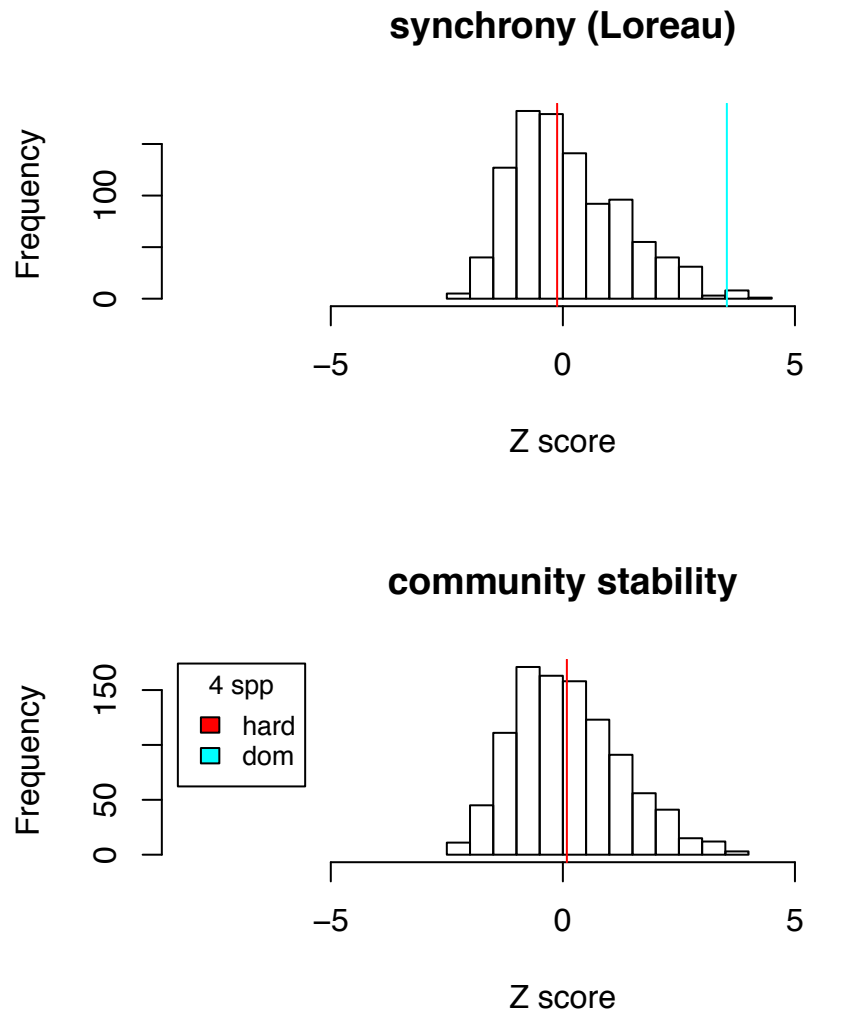
3. Figure S1 Time series of annual abundances of combined guild members. Abundance data are transformed ( $\log_{10}(x+1)$ ) prior to plotting.



#### 4. Figure S2 Summary of randomisation tests.



5. Figure S3 Z scores for observed guilds from a null distribution using a cyclic shift randomisation, in relation to the distribution of Z scores obtained using synthetic guilds of equivalent S (300 runs).

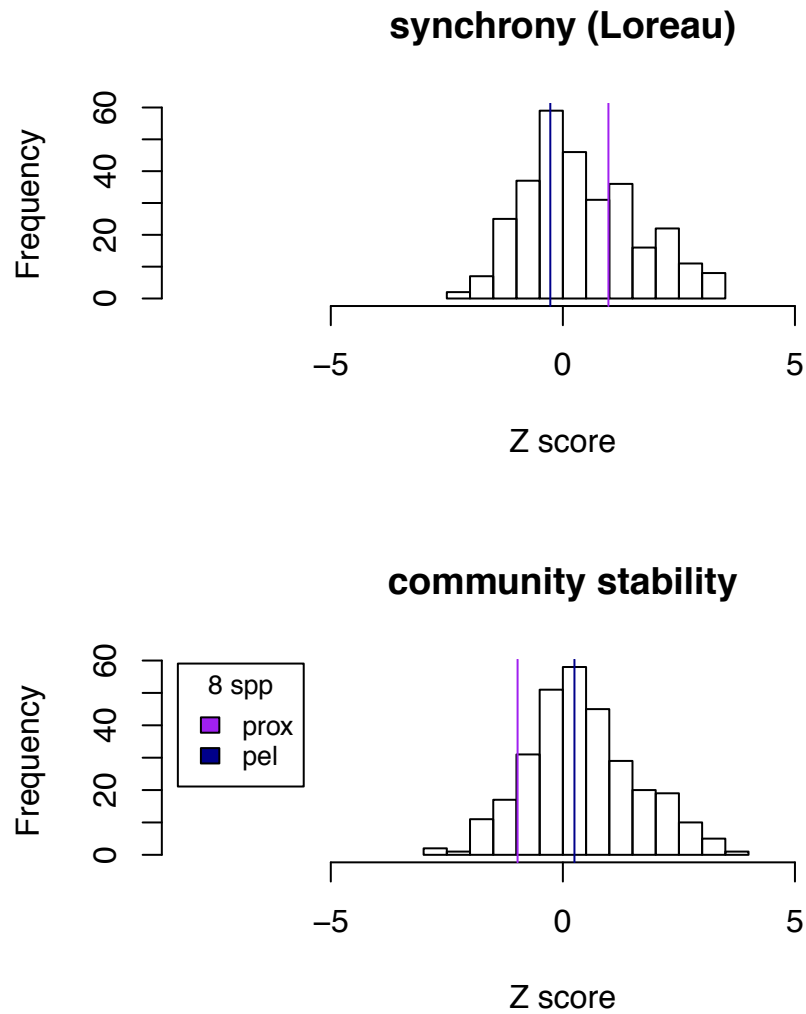


Z scores

dominant (dom) species: Loreau  $Z=3.65$ ; dominant species: stability  $Z=6.79$

hard benthic (hard): Loreau  $Z= -0.152$ ; hard benthic stability  $Z=0.113$

Figure S3 continued

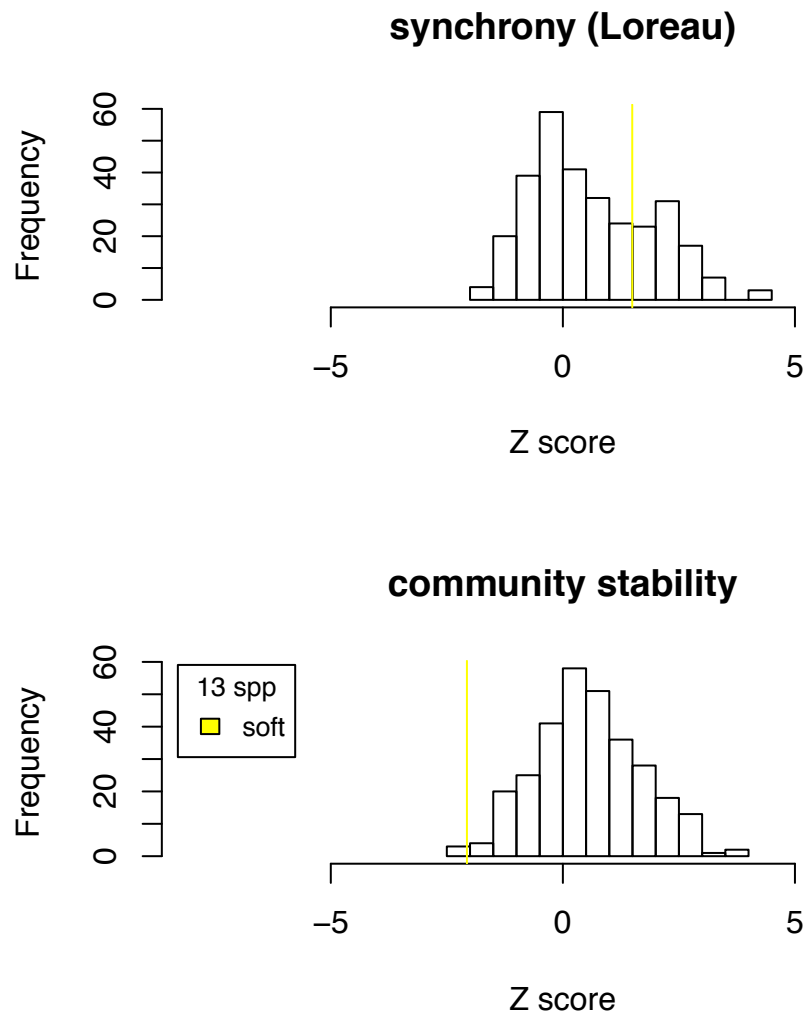


Z scores

proximo benthic (prox): Loreau  $Z=0.98$ ; proximo benthic: stability  $Z=-0.975$

pelagic (pel) Loreau  $Z=-0.271$ ; pelagic: stability  $Z=0.249$

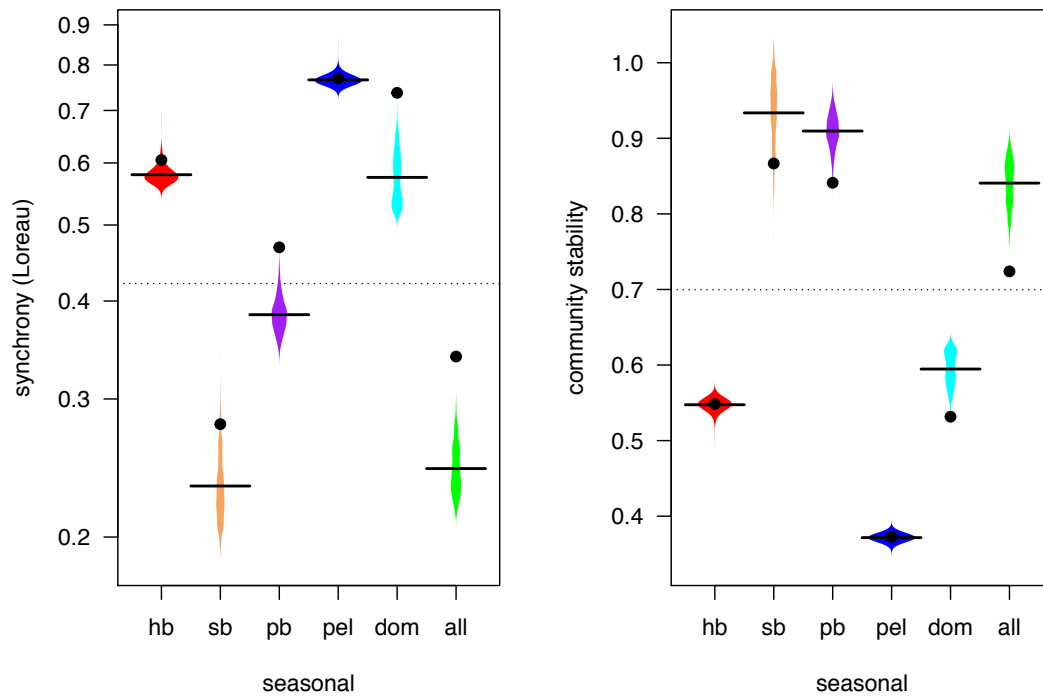
Figure S3 continued



Z scores

soft benthic (soft) Loreau 1.22; soft benthic: stability  $Z = -1.15$

6. Figure S4. Synchrony and community stability analysis using monthly data. The analysis presented in Figure 1 was repeated using the entire time series ( $t=442$  time points, with  $n=300$  runs). In each case a black dot represents the observed value. The quantiles of these are as follows: synchrony: hb=0.94, sb=0.94, pb=1, pel=0.70, dom=0.99, all=1; stability: hb=0.51; sb=0.10; pb=0.003; pel=0.71; dom=0.01; all=0.



8. Figure S6 Distribution of correlation coefficients (Pearson), showing temporal correlation between pairs of species in group or guild of interest. Note that the temporal abundances of species tend to positively covary (there are good years and bad years) and that this is notably strong for dominants.

